ON THE GENUS *LYCOPTERA* AND ITS RELATIONSHIP WITH THE FAMILY HIODONTIDAE (PISCES, OSTEOGLOSSOMORPHA)

BY

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INTRODUCTION

The Lycopteridae, a family of small (< 12 cm) upper Jurassic–lower Cretaceous teleosts, are widely distributed in lacustrine deposits of eastern Siberia, Mongolia and China (from 36°–56°N, and 96°–134°E).

Until Yakovlev's (1965) recent revision, the systematics of this family were in some disorder, with at least sixteen nominal species referred to the genus *Lycoptera*. In addition, a number of rather ill-defined genera were also recognized. Yakovlev's critical study suggests that there are only two species of *Lycoptera* (*L. middendorffi* Müller, 1848, and *L. fragilis* Hussakof, 1932), and that three other and monotypic

genera should also be recognized (*Manchurichthys*, *Sinolycoptera* and *Mesoclupea*). Compared with *Lycoptera* these genera are poorly studied, and contribute little to understanding the phyletic relationships of the family. Thus, for the purposes of this paper references to the lycopterids are, in fact, to the genus *Lycoptera* itself.

Apart from Reis' (1910) observations on the otoliths of *Lycoptera middendorffi* (and some notes on vertebral structure by Saito [1936]), no really comprehensive anatomical study appeared until Berg's revision of the family was published in 1948. Thus it is not surprising that the systematic position of the Lycopteridae has been in some doubt ever since the family was defined by Cockerell (1925). Yakovlev's (*op. cit.*) remarks that " *Lycoptera* has to this day remained the most interesting and enigmatic fish of the Asian Mesozoic ", are fully justified, particularly when it is recalled that *Lycoptera* has been considered the ancestor or near ancestor of the Cyprinidae. If this relationship could be accepted, then the lycopterids might also throw some light on the origin of the largest and most diverse group of freshwater fishes, the Ostariophysi.

It was mainly from this viewpoint (see Rosen and Greenwood, 1970) that I began to study the Lycopteridae in detail. Soon it became clear, however, that the lycopterids and the cyprinids (or for that matter any member of the Ostariophysi) were in no way related, a conclusion reinforced by the appearance of Gaudant's (1968) paper dealing at length with the anatomy of *Lycoptera davidi* (= *L. middendorffi*).

Several features in the osteology of *Lycoptera* suggested a relationship with the osteoglossomorph family Hiodontidae. It is the object of this paper to review the osteology of *Lycoptera* (particularly since I disagree with Gaudant [*op. cit.*] on certain points), and in the light of that review to compare the two families and reconsider the various proposed relationships of the Lycopteridae.

The only fossil hiodontid, *Eohiodon rosei* (Hussakof), from the middle Eocene beds of British Columbia (see Cavender, 1966a) closely resembles *Hiodon* in most anatomical features. References to *Hiodon* thus include *Eohiodon* as well as the two extant species of *Hiodon*, *H. alosoides* and *H. tergisus*. Where *Eohiodon* resembles, or departs from *Lycoptera* more than does either *Hiodon* species, then it will be given particular mention.

A COMPARISON OF *LYCOPTERA MIDDENDORFFI* WITH *HIODON* AND *EOHIODON* SPECIES

Study material : Information on *Lycoptera* osteology was derived principally from eight well-preserved specimens of *L. middendorffi* in the collections of the British Museum (Nat. Hist.) Palaeontology Department (specimen numbers P16967a and b, and P20930) ; forty-eight less well-preserved specimens from the same slabs also provided some information, as did three specimens kindly loaned to me by the Munich Museum.

Most of the *Hiodon* material examined is of *H. alosoides* (27 specimens) but some *H. tergisus* (11 specimens) were also studied ; dissections, dried skeletons, alizarin transparencies and radiographs were used. The size range of these fishes is 2·5 to 26·0 cm standard length. All are from the B.M. (N.H.) collections.

Neurocranium (Text figs. 1 to 4). The nature of the *Lycoptera* fossils is such that

it is impossible to prepare a complete, three-dimensional neurocranium. Consequently, any comparison is restricted to superficial regions of the skull. It is particularly regrettable that no observations could be made on the otic regions of the skull in these fishes since the otic region provides a highly characteristic and specialized feature of the hiodontids (Ridewood, 1904 ; Greenwood 1963, and in preparation).

Nasals. These bones are not well-preserved in most specimens. The few that I have been able to examine are narrow, slightly curved, gutter-like elements closely associated with and separated by the median ethmoid.

In *Hiodon*, the nasals are tubular, and more strongly curved (indeed, are angled). As in *Lycoptera* they are associated with the median ethmoid, and posteriorly are in contact with the frontals.

Gaudant (*op. cit.*) likens the nasals of *Lycoptera* to those of *Elops saurus*, but in my opinion they are more like those of the Mormyridae. In *Elops* (and other elopoids, see Nybelin 1956 and 1967) the sensory canal is contained within a tube provided with four pores, and the base of the nasal is expanded to a greater (*Elops* and *Megalops*) or lesser (*Tarpon*) degree. In contrast, the mormyrid nasal is an open gutter (personal observations ; Taverne 1968 and 1969 ; Ridewood, 1904).

Yakovlev (1965) on the other hand, describes the nasals of *Lycoptera* as " . . . contiguous and not divided by the frontal bones . . . , even in the posterior third . . . " I would agree that the frontals probably do not separate the nasals, but in no specimens can I find evidence of the nasals being contiguous at any point. Judging from the shape of the anterior frontal tips it is even possible that a short region of each frontal lies between the posterior part of the nasals (personal observation ; and see Gaudant's plate 4, figs. 1 and 2). The supposed contiguity of the nasals is one of the reasons why Yakovlev (*op. cit.*) thought that *Lycoptera* might be related to the osteoglossids (see page 282).

Median ethmoid : Lying between the nasals is a relatively small, almost rectangular bone identified as a rostral by Berg (1948), and as a rostro-postrostral by Gaudant (*op. cit.*). Yakovlev (*op. cit.*) refers to a rostral in *Lycoptera* (but gives no description of the bone), and uses its presence as part of an argument to show that the ethmoid region in *Lycoptera* is more primitive than in *Leptolepis coryphaenoides*.

From my own observations (on admittedly few and, for that region, poorly preserved specimens) and from Gaudant's figures and plates, I can see no reasons for identifying the bone as a rostral (see Gardiner, 1963 and Nybelin 1967 for discussion). There is no trace of a transverse rostral commissure (*pace* Berg, *op. cit.*), nor does the arrangement of the circumorbital bones suggest that one was present. Gaudant (*op. cit.*) tentatively identifies, in one of his specimens, an ethmoidal pit line, but in none does he mention a tubular commissure ; none is visible in any of his figures.

Thus, I would propose that this bone be identified as a median ethmoid. Its shape and spatial relationships are like those of the median ethmoid in *Hiodon*.

Orbital region (Text figs. 1 and 2). Little can be learned about the orbital region in *Lycoptera*. The orbitosphenoid is somewhat smaller than in *Hiodon* ; the pterosphenoid and basisphenoid have not been clearly defined although faint indications of both are sometimes visible.

A long, splint-like supraorbital bone has been identified by Berg (1948) and by Liu

et al (1963). Gaudant (*op. cit.*), however, failed to find this element, and I would agree with his conclusion that it is wanting in *Lycoptera*. *Hiodon*, too, lacks a supra-orbital (as do all the Osteoglossomorpha).

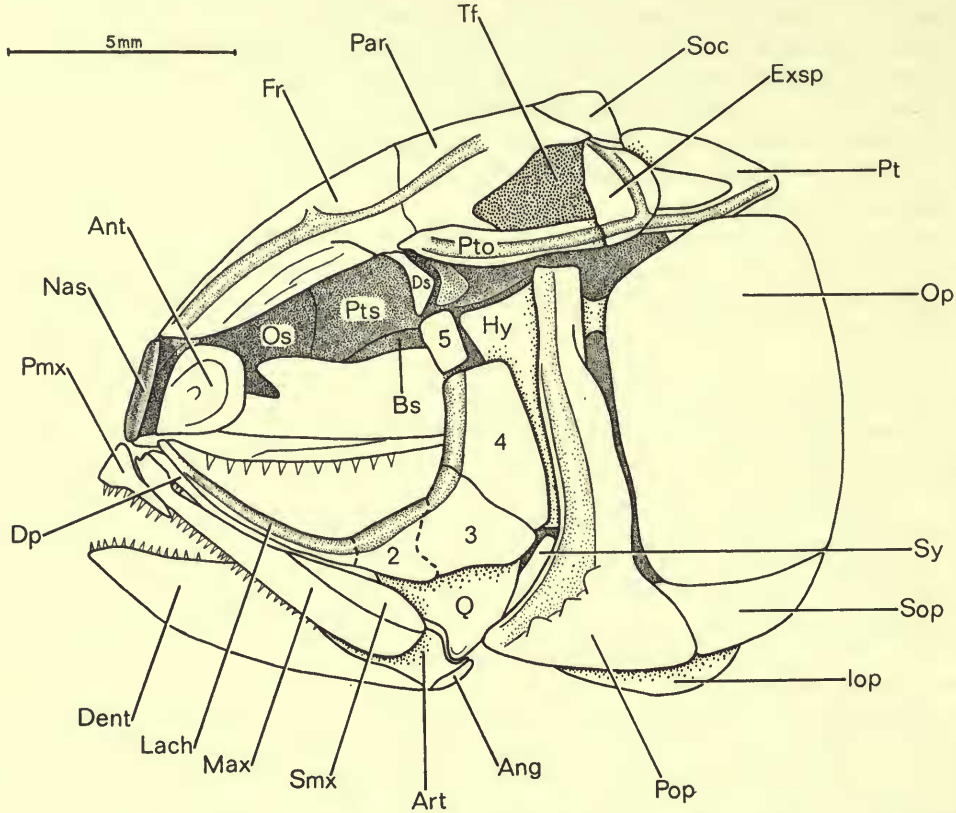

FIG. 1. *Lycoptera middendorffi*. Skull slightly restored ; based mainly on specimen B.M. (N.H.) P20930 I. Lateral line canals of extrascapular from Berg (1948) and Gaudant (1968) ; canals in dentary omitted. The endopterygoid is not shown. The margins of the 2nd infra-orbital bone are indicated by dotted lines.

Ang. angular ; Ant. antorbital-prefrontal ; Art. articular ; Bs. basisphenoid ; Dent. dentary ; Dp.? dermopalatine ; Ds. dermosphenotic ; Epi. epiotic ; Exsp. extrascapular ; Fr. frontal ; Hy. hyomandibula ; Ic. intercalar ; Iop. interoperculum ; Lach. lachrymal ; Max. maxilla ; Meth. median ethmoid ; Mth. metapterygoid ; Nas. nasal ; Op. operculum ; Os. orbitosphenoid ; Par. parietal ; Pmx. premaxilla ; Pop. preoperculum ; Pt. post-temporal ; Pto. dermopterotic ; Pts. pterosphenoid ; Q. quadrate ; Smx. supramaxilla ; Soc. supraoccipital ; Sop. suboperculum ; Sy. symplectic ; Tf. temporal fenestra. 2–5. 2nd to 5th infraorbitals.

Frontals : (Text figs. 3 and 4). In their general outline and relative contribution to the dorsicranium, the frontals of *Lycoptera* and *Hiodon* are similar (see below, p. 271, regarding the sensory canal systems). Whether or not in *Lycoptera* the anterior tips of the frontals lie between the nasals, is uncertain (see above, p. 261).

Parietals (Text figs. 3 and 4). The entire outline of these bones is not clearly defined in any of the B.M. (N.H.) specimens. However, from the observations I could make, I would agree with the restorations figured by Gaudant (*op. cit.*). The shape

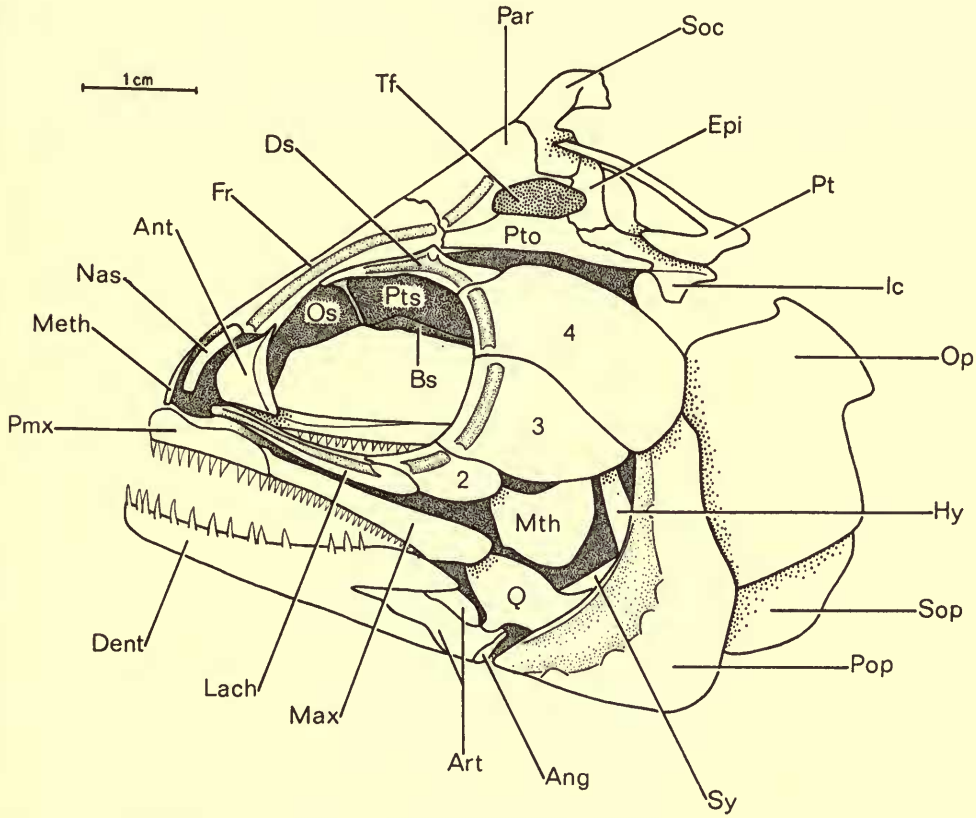

FIG. 2. *Hiodon alosoides*. Skull. Endopterygoid, and lateral line canals of dentary omitted. The extrascapular has been removed to show the parietal, and the temporal fenestra. Abbreviations as in fig. 1.

of the parietals in *Lycoptera* and *Hiodon* is not markedly different. But, in *Hiodon* the supraoccipital is a much larger bone with a greater anterior extension ; consequently the area of medial contact between the parietals is much less than in *Lycoptera* (*cf.* text figs. 3 and 4).

Temporal fenestra. A large temporal fenestra is visible in all B.M. (N.H.) specimens of *Lycoptera* in which that region of the skull is well-preserved. Gaudant (*op. cit.*) also found this opening in his material. Liu *et al* (1963), however, illustrate the dorsicranium of a specimen (size not stated) in which no fenestra is present. Gaudant suggests that Liu's fish may be a very large individual, and that with growth the bones surrounding the fenestrae encroach upon, and eventually obliterate the openings completely. No specimens with fenestrae in an intermediate stage of

closure have been illustrated or noted, and there remains the possibility that Liu *et al* overlooked the fenestrae in their material. Even in the best specimens the fenestral outline is faint.

Gaudant (*op. cit.*) describes the temporal fenestra as being bordered by the parietals, dermopterotic, extrascapular and supraoccipital. Some of these bones are undoubtedly associated with the fenestra, but since the extrascapular lies above the opening (text figs. 1 and 3) it can hardly be considered one of the delimiting bones. Also, from my own observations I am uncertain whether the supraoccipital is involved. A small area of the medial margin, which Gaudant identifies as part of the

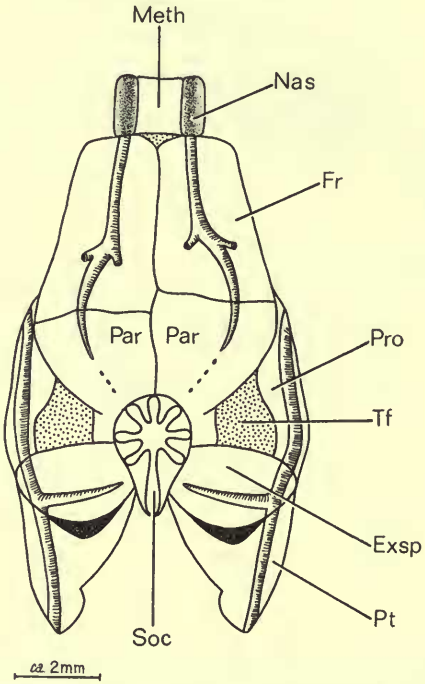

FIG. 3. *Lycoptera middendorffi*. Dorsicranium. Modified after Gaudant (1968). Abbreviations as in fig. 1, except Pro. pterotic.

supraoccipital, appears to be a narrow, posterior prolongation of the parietal (see text fig. 3). Finally, I would identify the posterior boundary of the fenestra as being the epiotic ; from Gaudant's figure and description he implies that the extrascapular forms that border. In at least two B.M. (N.H.) specimens the extrascapular is displaced and the epiotic can be seen forming the hinder limit of the fenestra.

The significance and homology of the temporal fenestra are difficult to establish. As Ridewood (1904) noted, it would appear to correspond with the preepiotic fossa found in most clupeoid fishes. This fossa is a small but deep pit lying immediately anterior to the epiotic, and is formed by an invagination from the parietal, epiotic and autopterotic. There are, however, differences in the two structures. The clupeoid preepiotic fossa usually ends blindly against the deeper part of the supraoccipital

and is a distinct pit in the bones involved. The temporal fenestra does not involve invagination of the bones, and if it were not closed by cartilage, would open directly into the cranial cavity.

A temporal fenestra similar to that of *Lycoptera*, (albeit less extensive) occurs in *Hiodon*, where it is occluded by a plug of cartilage. In *H. alosoides* the fenestra is largest in small fishes, but is still clearly visible in the largest specimen examined (26 cm S.L.). It is filled by a slip of epaxial body musculature and the whole area is covered by the greatly expanded extrascapular (*cf. Lycoptera* where the extrascapular only covers the posterior quarter of the fenestra.)

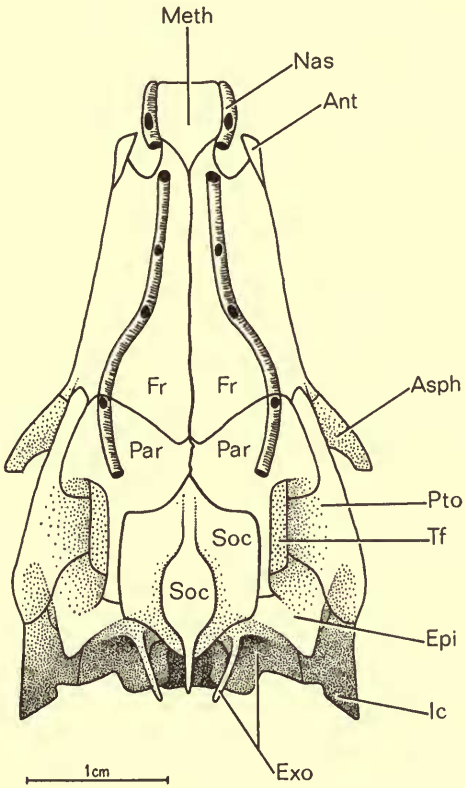

FIG. 4. *Hiodon alosoides*. Dorsicranium. The plane of orientation is such that a line drawn through the centre of the basioccipital facet to the vomer, would be horizontal. Asph. autosphenotic ; Exo. exoccipital. Others as in fig. 1.

As Gaudant (*op. cit.*) points out, the temporal fenestra is an unusual character, and one not found in any other Mesozoic teleost. Indeed, *Lycoptera* and *Hiodon* would appear to be the only primitive teleosts in which a temporal fenestra is developed (see also Greenwood, 1963). The large cartilaginous area in the temporal region of salmonoid and galaxioid fishes (the 'temporal fossa' of McDowall, 1969) resembles the temporal fenestra but is a more extensive, less well-defined area bordered by more (and

often intrasubordinally different) bones ; it would seem to be a correlate of the generally reduced ossification of the salmoniform skull.

Undoubtedly the development of a temporal fenestra (*Lycoptera* and *Hiodon*) or preepiotic fossa (Clupeoidei) is associated with the invasion of that part of the skull by epaxial body muscles. That a fossa is developed in clupeoids and a fenestra in *Hiodon* and *Lycoptera* may indicate that the structures are more probably analogous than homologous. Certainly there is no evidence from other characters to suggest a close relationship between the clupeoids and hiodontids (Greenwood, 1963 ; Greenwood *et al*, 1966).

In *Lycoptera* only the posterior part of the temporal fenestra is covered by the extrascapular, whilst in *Hiodon* the entire fenestra (and most of the parietal) lies beneath the expanded, scale-like extrascapular. Thus both the relative size, and the shape of this bone differ in the two genera. Another difference is the arrangement of the extrascapular latero-sensory canals. *Lycoptera*, according to Berg (1948) and Gaudant (*op. cit.*), had the posterior section of the temporal canal (*i.e.* the section between the posttemporal and the pterotic) passing through the lower part of the extrascapular (see text fig. 1). The branch forming the transverse commissure is given off near the hind margin of the bone, and runs medially in that position. (None of the B.M. (N.H.) specimens has this region of the skull sufficiently well-preserved to allow for first-hand observation on these points). In *Hiodon*, the branch from the posttemporal connects with the dermopterotic directly, and the extrascapular carries, near its posterior margin, the transverse commissure only. Both genera are alike in having the bony tube for the transverse commissure interrupted in the midline because the extrascapulars are separated by the supraoccipital. The gap is wider in *Lycoptera* than in *Hiodon*.

The otico-temporal region. The *pterotic* is an elongate and substantial bone in both genera. As far as I can determine, the temporal latero-sensory canal in *Lycoptera* is entirely bone enclosed ; in *Hiodon* the ventromedial aspect of the tube is open (Greenwood, 1963).

Virtually nothing is known about the occipital and lower otic regions of the *Lycoptera* skull, since that region is invariably covered by the collapsed operculum and associated bones.

From Gaudant's description and figures (especially plate 3) it is clear that the *supraoccipital* in *Lycoptera* is a smaller bone than in *Hiodon*, and that it does not separate the parietals for such a distance anteriorly. The supraoccipital crest in *Lycoptera* appears to be lower and probably does not have the characteristically " T " shaped section of *Hiodon*. However, judging from Gaudant's plate the crest may have a short-armed " T " section.

The presence of a moderately large supraocciptal in the *Lycoptera middendorffi* specimens figured by Gaudant (*op. cit.*) makes it the more difficult to understand the minute bone (not separating any part of the parietals, and hardly separating the extrascapulars) illustrated by Liu *et al* (1963, fig. 8). It will be recalled (p. 263) that these authors do not show a temporal fenestra in this fish, which Gaudant suggested might be a large individual in which the fenestrae had closed. Unfortunately Liu *et al* give no indication of the size of the specimen (nor any magnification for the

figure), neither do they discuss the supraoccipital in the text of their paper ; no dorsicranium is figured in the plates. That a fenestra might be obliterated by growth is a reasonable assumption, but it is improbable that parietal growth would almost cover the supraoccipital. I am inclined to think that Liu *et al*, probably influenced by the relationships of these bones in *Leptolepis*, have misinterpreted the situation in *Lycoptera* (*cf.* their drawings of these skulls in figure 8).

Skull base (Text figs. 5A and B). The *parasphenoid* is toothed in both genera with the teeth relatively larger and extending further posteriorly in *Hiodon* (and probably in *Eohiodon*). A small basipterygoid process is present in *Lycoptera*, but is absent in *Hiodon*. Gaudant (*op. cit.* plate 5, figs. 3 and 4) illustrates the posterior half of the parasphenoid in *Lycoptera middendorffi*, and clearly demonstrates its sharp upward angling (*ca.* 45°), a little posterior to the foramen for the internal carotid (see text fig. 5B). His photographs also show the relatively short, paired and near vertical ascending processes of this bone. These come into contact with the prootic, while the section running obliquely upwards forms the ventral, unpaired part of the base underlying the otico-occipital region of the skull.

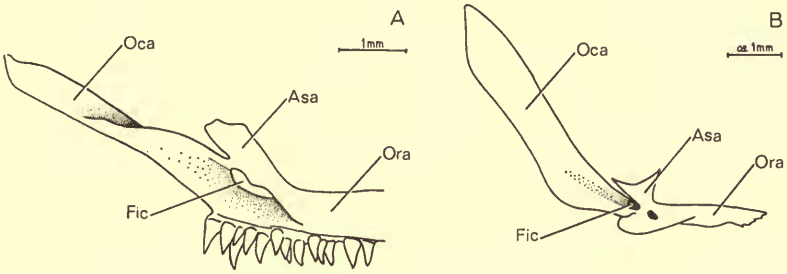

FIG. 5. *A. Hiodon alosoides.* Posterior part of a parasphenoid, viewed from the right. *B. Lycoptera middendorffi.* Posterior part of parasphenoid, viewed from the right (after Gaudant, 1968 : plate 5, fig. 4). Asa. ascending arm ; Fic. foramen for internal carotid artery ; Oca. occipital arm ; Ora. orbital arm.

The shape of the parasphenoid and the details of its morphology (except for the basipterygoid processes) are very similar in *Lycoptera* and *Hiodon* (see text fig. 5). Thus it seems reasonable to conclude that the ventral skull profile in *Lycoptera* had the same, peculiar " stepped " appearance as in *Hiodon*.

Otoliths (Text figs. 6 A-C). The peculiar otoliths of *Lycoptera middendorffi* were described and illustrated with great thoroughness by Reis (1910). In most of his specimens two of the three otoliths from each side (and sometimes from both sides) were preserved, if not *in situ*, at least closely associated with the skull. Accordingly Reis was able to determine the approximate spatial relationships of the otoliths, and on this basis to show that the asteriscus (lagenar otolith) is much larger than the sagitta (saccular otolith). From Reis' drawings and descriptions, the asteriscus is about 4 to 6 times longer than the sagitta. It also has an unusual, trapezoidal or unequally hexagonal outline. The shape of the sagitta is difficult to determine from the figures, but it appears to be trianguloid and without any marked sculpturing. The asteriscus, by contrast (text fig. 6C) has each face radially fluted over about half

its area, and there is at least one, short, crescentic groove at a point about two-thirds distant from the lower border (as orientated in the figures). Ornamentation seems to be more obvious on one face than on the other. No otolith was identified (or shown in a drawing) as a lapillus (utricular otolith) and Reis (*op. cit.*) makes no comments on its absence.

As Reis points out, it is most unusual among teleosts for the asteriscus to be larger than the sagitta, a condition otherwise found only in the Ostariophysi (and to a somewhat less marked degree in the Mormyridae, see Taverne, *op. cit.*) In both these groups, the shape of the sagitta and asteriscus is quite unlike their presumed counterparts in *Lycoptera*. Indeed, a large, hexagonal-trapezoidal asteriscus has, to the best of my knowledge, never been described from any other teleost group. Furthermore, the peculiar radial fluting of the *Lycoptera* asteriscus has not been described elsewhere.

Later workers (Saito, 1936 ; Takai, 1944 ; Berg, 1948 ; Liu *et al* 1963) do not describe otoliths from their material. When the otoliths are mentioned by these authors, it is always with reference to Reis' (1910) paper and figures. Gaudant (*op. cit.*) found otoliths in only one of the specimens he examined (L. *middendorffi*, B.M. (N.H.) reg. no. P273 [now P47792] ; but see below). His comments on *Lycoptera* otoliths, like those of his predecessors, are also based on Reis. (It should be noted that Gaudant reproduces one of Reis's drawing of an asteriscus but in the legend to the figure calls it a sagitta).

None of the B.M. (N.H.) specimens has the otoliths preserved, and I was unable to find them in specimen P47792 (where, according to Gaudant [*op. cit.*], they should be visible). I have tried to locate Reis' material, but without success. Apparently it is now either lost or destroyed. The absence of suitable material for otolith studies is the more regrettable because certain features of the otoliths described by Reis (*op. cit.*) suggest that his identification of the larger element as an asteriscus may be in error.

Compared with the sagitta, far less is known about intergroup variation in the shape of the teleost lapillus and asteriscus. Nevertheless, some generalizations on this subject are possible (based on Retzius, 1881 ; Frost, 1925–1930 ; Taverne, 1968 and 1969 ; and personal observations).

Apart from in the Ostariophysi and the Mormyriformes, the asteriscus is generally a flattened, slightly elongate, often kidney-shaped otolith with all or most of its margin deeply crenulate (often almost serrate) ; there is a deep and extensive sulcus on the median face. In the Ostariophysi and Mormyriformes the asteriscus is usually discoidal, the broad sulcus horseshoe-shaped, and the margin variously crenulate, serrate or smooth (or a combination of all three). A few ostariophysans have an elongate asteriscus which closely resembles the " typical " sagitta of other groups.

The angular, trapezoidal to hexagonal outline of the so-called asteriscus in *Lycoptera* has not yet been found in any teleost. Neither does the *Lycoptera* " asteriscus " have the prominent sulcus characteristic of that otolith in most (if not all) teleosts. Reis (*op. cit.*) attempts to identify a sulcus, but it is clear from both his description and figures that the feature he is dealing with is more in the nature of an elongate pit than the typically deep, extensive groove of the asteriscal sulcus.

A trapezoidal, or at least a noticeably angular outline appears to be more characteristic of the teleost lapillus (utricular otolith). Furthermore, that otolith does not show a well-developed sulcus, and its marginal ornamentation is often in the form of rather widely spaced radial grooves extending towards the centre of the otolith. On the upper face of the lapillus (near the region where the radial grooves converge) there is frequently a shallow, depressed area lying close to a low dome or ridge (text fig. 6A).

Altogether, the so-called asteriscus of *Lycoptera* shows more of the characters of a lapillus than an asteriscus. I am especially impressed by the resemblance between the *Lycoptera* " asteriscus " and the lapillus of *Hiodon alosoides* (*cf.* text figs. 6A and B with 6C, and with the figures in plate 2 of Reis, 1910). This resemblance includes the outline shape as well as many details of ornamentation, including the spaced radial grooves (more numerous over one half of the otolith) and the absence of a well-defined sulcus. Thus, I suspect that Reis misidentified the lapillus in *Lycoptera* as an asteriscus.

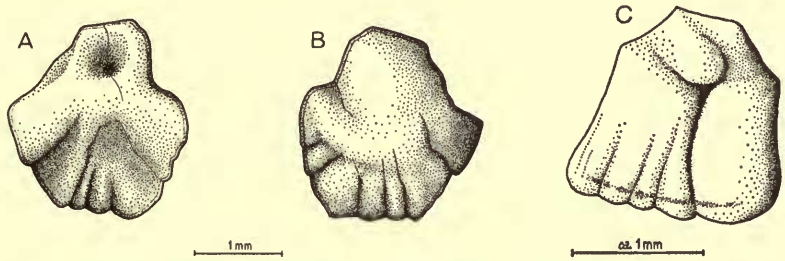

FIG. 6. A, B. *Hiodon alosoides*, lapillus in dorsal and ventral views. C. *Lycoptera middendorffi*, " asteriscus " (after Reis, 1910, plate 2, fig. 11)

There remains, however, the problem posed by the disposition of the otoliths as Reis has figured them in relation to the skull (Reis, *op. cit.*, plate 2). The problem is complicated by the lack of a third otolith in any specimen figured. In *Hiodon* the lapillus lies above and well anterior to the sagitta and asteriscus. One would, therefore, expect that in a fossil (even allowing for some *post mortem* dislocation) the lapillus should lie ahead and slightly above the other two otoliths (or the sagitta alone if that is the only lower otolith visible). In Reis' figures, the larger " asteriscus " is always shown behind the smaller otolith (his sagitta), and generally above it. The labyrinth of *Hiodon* is unusual in having the lapillus so far in advance of the sagitta ; in most fishes the lapillus lies above or even slightly behind the sagitta. If this latter condition was found in *Lycoptera*, then it would be possible for the sagitta to come to lie in front of the lapillus. Also, if *Lycoptera* had a large auditory fenestra (as in *Hiodon*) lateral to the sacculus, it seems even more likely that the sagitta could be displaced anteriorly during fossilization. The bone enclosed lapillus would be less subject to horizontal displacement.

I have of course assumed, as did Reis, that the smaller otolith is a sagitta. This point also remains to be clarified ; the figures and descriptions given by Reis (*op. cit.*) are not sufficiently clear for a decision to be made. The sagitta of *Hiodon alosoides*

is a most peculiar otolith and it should be possible to recognize its salient features in well-preserved fossils. All that can be said at present is that no features visible in Reis' drawings would immediately preclude the smaller otolith from being of the *Hiodon* sagitta type.

The so-called lycopteroid otoliths from the Mesozoic of Germany (Weiler, 1954, 1957 and 1965) are not closely similar to those of *Lycoptera middendorffi* (see page 283).

Circumorbital bones (Text fig. 1). Because the circumorbital series is generally not well preserved, little agreement has been reached on the number or the shape of these bones (*cf.* Berg, 1948, fig. 1 ; Liu *et al*, 1963, fig. 8 ; Gaudant, 1968, fig. 3.).

Berg (*op. cit.*) illustrates a single, elongate suborbital bone lying between the canal-bearing infraorbital series and the preoperculum. From Gaudant's (*op. cit.*) study, and from my own observations it is certain that Berg was in error. No suborbital is present ; the circumorbital series in *Lycoptera* is typically teleostean and is composed solely of canal-bearing infraorbital bones.

Judging from the two B.M. (N.H.) specimens (both on slab P20930) and from Gaudant's plate 2, fig. 1, Liu *et al*'s (*op. cit.*) restoration is the most accurate so far published. Certainly Gaudant's text fig. 3 is inaccurate in some respects. For example, the postorbitally situated infraorbitals are considerably wider than he depicts them, and the lachrymal (1st infraorbital) is much longer (see text fig. 1).

From my material I cannot be certain whether there are one or two bones lying below the orbit (Berg figures two and part of a third, Liu *et al* three, and Gaudant three and part of a fourth). Be that as it may, the first infraorbital (lachrymal) is a narrow, elongate bone deepening a little (or more definitely if there is no small second infraorbital) posteriorly. Behind the orbit there are two deep and wide bones, which extend backwards almost to the margin of the preoperculum. Above these it is difficult to determine the number or shape of the succeeding infraorbitals. In specimen P20930 there appears to be a short, barrel-shaped bone followed by an elongate, almost boomerang-shaped dermosphenotic.

Anteriorly, a large, shield-shaped antorbital is apparently fused with the prefrontal. Berg (1948) and Liu *et al* (1963) identify this bone as the lateral ethmoid, but it is clearly a canal bearing bone with another ossification lying medial to it (which I identify as being the prefrontal). My reason for thinking that the antorbital and prefrontal are fused is simply that the two bones (in all specimens I have examined) always have the same relative positions ; the other infraorbital bones are invariably displaced and variously disarticulated.

The bone Berg (*op. cit.*) identifies as a dermosphenotic (*i.e.* the uppermost infraorbital) is roughly triangular, as is the dermosphenotic in Gaudant's (*op. cit.*) restoration. A bone occupying a similar position in my best preserved specimen (P. 20930) is much narrower and is boomerang-shaped, the concave face directed anteriorly (text fig. 1). But, as there is only one specimen with a presumed dermosphenotic visible, I could well be mistaken on this point.

Regarding the total number of infraorbital bones (including the dermosphenotic and antorbital), Berg (*op. cit.*) finds 7 (*i.e.* interpreting his lateral ethmoid as an antorbital), Liu *et al* 6 (again interpreting the lateral ethmoid as an antorbital), and Gaudant (*op. cit.*) 6. However, Liu *et al* do not specifically identify a dermos-

phenotic (which they do in the *Leptolepis* they figure) ; from their drawing it seems likely that a 7th infraorbital (*i.e.* a dermosphenotic) is present. The count from specimen B.M. (N.H.) P20930 could be either 6 or 7 depending on whether or not the small " second " infraorbital is a preservation artefact.

Hiodon has a total of 6 infraorbital bones (Nelson, 1969). Although there is an overall similarity between *Hiodon* and *Lycoptera* in the shape of the entire series (narrow suborbitally, expanded postorbitally) there are differences in detail (*cf.* text figs. 1 and 2). The expanded postorbital bones are deeper in *Hiodon*, and the infraorbital preceding the dermosphenotic is expanded (short and narrow in *Lycoptera*). The antorbital in *Hiodon*, like that of *Lycoptera*, is fused with the prefrontal, and the dermosphenotic is an elongate, angled bone (larger than, but basically similar to *Lycoptera*).

Cephalic lateral line system (Text figs. 1 to 4). Superficially, the cephalic lateral line system is virtually identical in both *Lycoptera* and *Hiodon*. It is of the primitive type in which there is no connection between the supraorbital and temporal canals ; the infraorbital canal is connected, through the dermosphenotic, with the temporal canal in the dermopterotic, but the supraorbital system ends in the parietal. The supraorbital canal has medial and lateral branches in *Lycoptera*, but these are not developed in *Hiodon*.

Other differences concern branching of the infraorbital system. In *Hiodon* this canal divides in the dermosphenotic, one branch curving backwards to join the temporal canal, the other and longer branch running forward in the dermosphenotic below and parallel with the supraorbital canal in the frontal. No such dichotomy has been described in *Lycoptera*.

In *Hiodon*, the pterotic portion of the temporal canal is open medially for much of its length (Greenwood, 1963) and forms part of what appears to be a pseudo *recessus lateralis* (in connection with which other bones, including the hyomandibula, are modified ; personal observations). Unfortunately the nature of the pterotic canal cannot be determined in *Lycoptera* (or in *Eohiodon*).

Opercular series (Text figs. 1 and 2). The *preoperculum* of *Lycoptera*, compared with that of *Hiodon*, and especially *Eohiodon*, has a more pronounced posterior prolongation of its lower, horizontal arm which is also shallower than in *Hiodon*. The vertical arm is longer, and reaches the pterotic ; in *Hiodon* there is a distinct gap between the two bones. Expressed in another way, the preoperculum in *Lycoptera* extends vertically beyond the hyomandibula head, whereas in *Hiodon* it barely reaches the level of the opercular process on the hyomandibula.

The *operculum* of *Lycoptera* is a relatively larger bone and extends further dorsally than it does in *Hiodon* ; in that genus its upper margin is excavated, not rounded as in *Lycoptera*.

The *interoperculum* of *Lycoptera* appears to be more ventrally situated because it is visible in lateral view, whereas in *Hiodon* it is hidden behind the ventral limb of the preoperculum. There are also differences in the shape of the *interoperculum*. In *Hiodon* the bone is almost rectangular, is narrow and nearly as long as the horizontal arm of the preoperculum. In *Lycoptera* it is relatively shorter (about half the length of the preoperculum), is somewhat deeper, and has a curved lower margin.

The *suboperculum* is similar in both genera.

Hyoid arch (Text figs. 7A and B). The hyoid arch of *Lycoptera middendorffi* has been described in great detail by Gaudant (*op. cit.*). The *hyomandibula* differs from that of *Hiodon* in several respects. Both, however, have a very well-developed opercular process, but this is probably of little significance since a large process is found in such unrelated groups as the esocoids and gadoids, as well as in the osteoglossoids and notopteroids. *Lycoptera* has a single articular head to the hyomandibula ; in *Hiodon* this surface is double with a large but bridged gap between each head (an arrangement probably correlated with the pseudo *recessus lateralis* mentioned above).

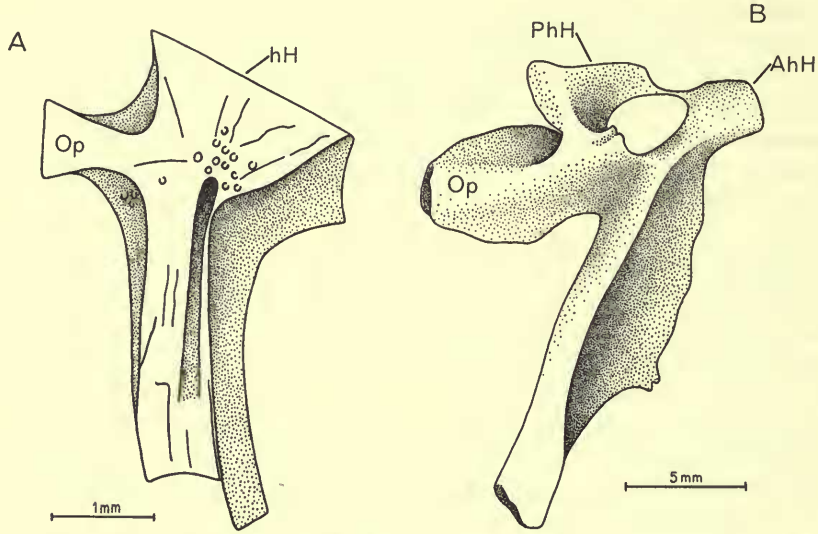

FIG. 7. A. *Lycoptera middendorffi*. Right hyomandibula, lateral aspect (after Gaudant, 1968). hH. head of hyomandibula ; Op. opercular process. B. *Hiodon alosoides*. Right hyomandibula, lateral view. AhH. anterior head ; PhH. posterior head ; Op. opercular process.

The shape of the *ceratohyal*, as well as the shape, number and disposition of the branchiostegal rays (especially the three, curved, broad upper rays) are closely similar in both *Lycoptera* and *Hiodon*. It may be noted in passing that in these characters neither genus resembles either the elopoid or clupeoid types ; perhaps the closest resemblance is to the notopterid and mormyrid types (McAllister, 1968).

Gaudant (*op. cit.*) describes and figures a single *hypohyal* in his specimens, but Berg (1948) found two small hypophyals. Unfortunately, this area of the hyoid arch is not clearly visible in any B.M. (N.H.) specimens. *Hiodon* has a pair of hypophyals on each side.

Both genera have a well-developed *basihyal dentition*, but the shape of the basihyal and its tooth plate are not known in *Lycoptera*. This is regrettable, since Nelson (1968) has drawn attention to the peculiar (and apparently characteristic) shape of

the tooth plate in *Hiodon* ; a similarly shaped plate is otherwise only known from the related Notopteridae (Nelson, *op. cit.*).

Palatopterygoid arch (Text figs. 1 and 2). Again, it is from Gaudant's (*op. cit.*) work that the most detailed descriptions are available (see his text fig. 8).

The *metapterygoid* of *Hiodon* is relatively smaller than that in *Lycoptera,* and is kidney-shaped, without the antero-dorsally directed flange which overlaps the endopterygoid in *Lycoptera.*

Gaudant (*op. cit.*) identifies a small, toothless bone lying above the ectopterygoid (and immediately anterior to the endopterygoid) as a *dermopalatine.* If he is correct (which I doubt), then *Lycoptera* differs from *Hiodon* where the dermopalatine is toothed, and lies anterior to—and is in a linear series with—the ectopterygoid. One B.M.(N.H.) specimen, P20930, shows medially and a little above the dorsal margin of the maxillary head, a short length of toothed bone (see text. fig. 1). It seems reasonable to identify this bone as the dermopalatine ; if this is correct, then it is similar to the dermopalatine of *Hiodon.*

The *ectopterygoid* is toothed in *Hiodon,* toothless in *Lycoptera* ; the *endopterygoid* is toothed in both genera.

The *quadrate* has a similar shape and proportions in both *Hiodon* and *Lycoptera.*

Jaws (Text figs. 1 and 2) There is an overall similarity in the upper and lower jaw elements of both genera.

The *premaxilla* is a small bone without traces of an ascending process ; it is relatively longer in *Hiodon,* and its articulation with the maxilla is a more intimate junction in that genus.

The *dentary* in *Hiodon* is more slender, and the coronoid region is shallower than in *Lycoptera.* I do not agree with Gaudant's (*op. cit.*, fig. 9) figure of the *articular.* In B.M. (N.H.) specimens the joint surface of the articular is a deep and clearly defined notch (not, as he shows it, an elongate concavity) closely fitting around the quadrate head.

The *angular* is a small bone in both genera. According to Ridewood (1904) there is no angular in *Hiodon,* but it is present in all the alizarin preparations I have examined.

A single *supramaxilla* is present in *Lycoptera,* but absent in *Hiodon.*

Gular plate. A large gular plate is present in apparently both species of *Lycoptera.* No trace of this bone was found in any of the many *Hiodon* specimens examined.

Vertebral column. Saito (1936) has given a detailed description of the vertebrae in *L. davidi* (= *L. middendorffi*) to which little can be added. Saito was also the first to detect ontogenetic changes in the centra, which are diplospondylous in small individuals but mostly monospondylous in larger fishes (> 50 mm S.L.).

According to Saito (*op. cit.*) and Gaudant (*op. cit.*), the neural and haemal arches of caudal vertebrae are fused with the centrum (neither author mentions the condition in abdominal vertebrae). In my material of *L. middendorffi* (size range 40–55 mm S.L.) I find that the first four preural vertebrae have autogenous haemal arches, but that haemal arches on the more anterior vertebrae are fused with the centra in fishes > 45 mm S.L. ; in smaller fishes all the haemal arches appear to be autogenous.

Gaudant (*op. cit.*) describes both epineural and epicentral intermuscular bones (the

latter he calls epipleurals although they are in no way associated with the pleural ribs). Other authors (except Takai [1944] who failed to locate intermuscular bones in some specimens) mention only one pair of intermuscular bones per vertebra, but differ in their opinions as to whether the bones are epineural or epicentral in position ; all agree that intermuscular bones are not present posteriorly beyond the first four or five caudal vertebrae. Takai's confused nomenclature for structures associated with the vertebrae has been clarified by Yakovlev (1965), who shows that, in fact, one pair of intermuscular bones is present in all the *Lycoptera* " species " studied by Takai (*op. cit.*)

From the B.M. (N.H.) material studied, I would identify the intermuscular bones as epineurals. This material also suggests how Gaudant (*op. cit.*) came to describe both epineurals and epicentrals. The epineurals in *Lycoptera* are very elongate bones, and thus extend backwards across several vertebrae. If the distal end of the epineural is displaced ventrally (or the tip is broken off and slips downwards) it can look much like a short intermuscular bone arising from a centrum behind that from which it actually stems. Careful examination, however, usually enables one to trace the " epicentral " back to its origin as an epineural on an anterior vertebra.

The pleural (ventral) ribs articulate with the tips of the broad-based, triangular parapophyses fused with the centra.

In *Hiodon*, the vertebral centra are somewhat stouter structures than those of *Lycoptera*, but are essentially of the same primitive type with a relatively large notochordal foramen. No trace of diplospondyly can be detected, even in the smallest specimen examined (*H. alosoides* 25 mm S.L.) ; it would be of great interest to know something about the ontogeny of the vertebrae in *Hiodon*.

More neural arches are autogenous in *Hiodon* than in *Lycoptera* (the condition is unknown in *Eohidon*), since the arches of all abdominal vertebrae are free from their centra, as are the first two caudal neural arches. All haemal arches except those of the first and second preural centra and the first ural centrum, are fused to the centrum. As in *Lycoptera*, the left and right halves of each abdominal neural spine are usually separate, even in large fishes (*i.e.* 25 cm S.L.) ; in caudal vertebrae, however, the spine is always a single structure (separate halves are common in the anterior caudal vertebrae of *Lycoptera*, and occasionally occur in the posterior vertebrae as well).

The parapophyses in *Hiodon* are fused with the centra but are elongate and dagger-shaped. In contrast with *Lycoptera*, the pleural ribs articulate directly with the centrum a little behind the shaft of the parapophysis (Greenwood, 1963).

Yakovlev (*op. cit.*) tabulated the various counts obtained for the number of vertebrae in *Lycoptera* " species " and warned of the difficulties in obtaining exact figures (diplospondyly, state of preservation, etc.). The counts for total number of vertebrae range from 43–50 (No indication is given of whether or not all the vertebrae associated with the caudal fin skeleton are included in these totals) ; 18–24 anterior vertebrae carry pleural ribs, the first rib being associated with the third centrum. *Hiodon* (*i.e.* both species) has 55–58 vertebrae (excluding the two ural centra), of which 27 or 28 bear ribs (Data from 9 specimens) ; the first rib is associated with the third vertebra. Even allowing for difficulties in obtaining accurate counts in

Lycoptera it is reasonable to conclude that *Hiodon* has more vertebrae and ribs. (Another lycopterid, the monotypic genus *Sinolycoptera langshanensis* resembles *Hiodon* in having 58 vertebrae [Yakovlev, *op. cit.*]). *Eohiodon*, with 49 vertebrae has a lower count than either *Hiodon* species, and thus more closely resembles *Lycoptera*, although it may have slightly more caudal vertebrae (*ca.* 25, *cf.* 20–23 in *Lycoptera*); no information is available on the number of pleural ribs in *Eohidon* (Cavender, 1966a).

Both *Lycoptera* and *Hiodon* have slender and elongate supraneurals lying between the neural spines of all vertebrae from in front of the first, until about the second vertebra behind the dorsal fin origin.

Caudal fin skeleton (Text figs. 8, 9 and 10) Besides a few comments by Berg (1948) on the number of hypurals and epurals, no author before Gaudant (*op. cit.*) paid much attention to the caudal fin skeleton in lycopterids. The figures in Reis (1910), Saito (1936), Takai (1944) and Liu *et al* (1963) are schematic and provide no critical information. Liu *et al* (*op. cit.*) describe the caudal fin in *L. muroii* (a synonym of *L. middendorffi*) as a " . . . somewhat advanced character " (relative to other " species " of *Lycoptera*) but do not list any specific reasons for their statement.

Gaudant (*op. cit.*, pp. 26–28, fig. 14) gives a detailed figure and description, as well as an excellent photograph of the specimen on which these were based (see plate 2, fig. 2). As figured by Gaudant, the caudal skeleton of *L. middendorffi* resembles the elopoid type (Nybelin, 1963) but with certain differences.

Salient features in Gaudant's restoration are : a separate second ural centrum, seven hypurals, three epurals, a fully-developed neural spine on the first pre-ural vertebra, a reduced spine on the first ural vertebra, and the uroneurals (called urodermals by Gaudant) arranged in two sets (a lower one of three elongate bones, and an upper set of two [one moderately long, and other short]). This uroneural arrangement is peculiar. It is neither of the elopoid type (three lower and a single upper bone lying at an angle to, and overlapping the former), nor of the leptolepid type (lower set of four and an upper of three short bones with at least the first overlapping the lower set) ; see Nybelin (1963) and Patterson (1967). The alignment and size of the upper uroneural (Ur 5) in Gaudant's figure does not accord with any known teleost caudal skeleton type (see Monod, 1968), nor does the arrangement of a small upper uroneural lying below an elongate one.

I have examined six well-preserved caudal fin skeletons of *L. middendorffi*, *ca.* 45–50 mm S.L., and find that I disagree with Gaudant on two major points. It might be added that I find the specimen illustrated in Gaudant's plate (*op. cit.*, plate 2, fig. 2) to be essentially like those I have examined.

In the B.M. (N.H.) fishes there is a single epural (not 3) closely associated proximally with the short neural spine on the first ural vertebra (see text fig. 9). The second point of disagreement concerns the number, shape and disposition of the uroneurals. In all B.M. (N.H.) specimens I find only a single series composed of three or four elongate bones, the first three being of approximately the same length, the fourth somewhat shorter.

I suspect that Gaudant has confused with epurals the proximal ends of caudal fin rays, the bifid neural spines of preural vertebrae, and possibly, fragments of uro-

neurals. The uroneural arrangement he describes is probably the result, in part, of the uroneurals being broken and displaced. His " urodermal 5 " in plate 2, fig. 2, and in text-fig. 14, certainly looks like the distal portion of the 2nd or 3rd uroneural.

In other respects Gaudant and I agree on the anatomy of the caudal fin skeleton. We both find that there is a total of 18 principal caudal fin rays (1 unbranched and 8 branched rays in each lobe). The articulated fin rays of the upper lobe are preceded by about 10-spine-like procurrent rays ; there are 8 procurrent rays in the lower lobe.

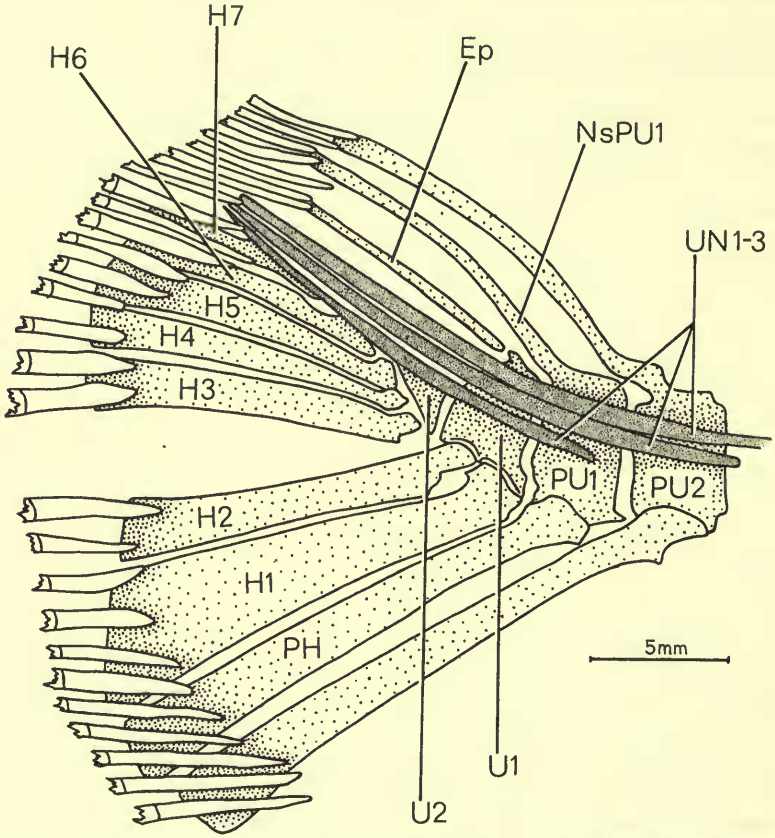

FIG. 8. *Hiodon tergisus.* Caudal fin skeleton, drawn from a radiograph of B.M. (N.H.) reg. no. 1862. 11. 18 : 45. For abbreviations see fig. 9.

Two of the six B.M. (N.H.) specimens have an interesting condition of the vertebrae associated with the 1st and 2nd hypurals (text fig. 10). Instead of there being a single first ural centrum carrying both hypurals, each hypural articulates with a separate centrum. The first caudal centrum carries a neural arch and short spine, the second an arch and very reduced spine. A third specimen (of about the same length as the other two, *ca.* 45 mm S.L.) has these two centra fused but with the fusion line still visible ; it resembles a caudal vertebra in the intermediate stage between diplo- and monospondyly. Those specimens with two distinct parts to the

" first " ural centrum also have a greater degree of displospondyly in the caudal vertebrae. Presumably the double " first " ural represents an early stage in the ontogeny of the usual compound first ural centrum. At first sight the double " first " ural centrum condition might be interpreted as comparable with the diplospondyly which occurs throughout the vertebral column in small fishes, and becomes progressively confined to the caudal region in larger individuals. However, there is an important difference between the two ural elements and a pair of hemicentra

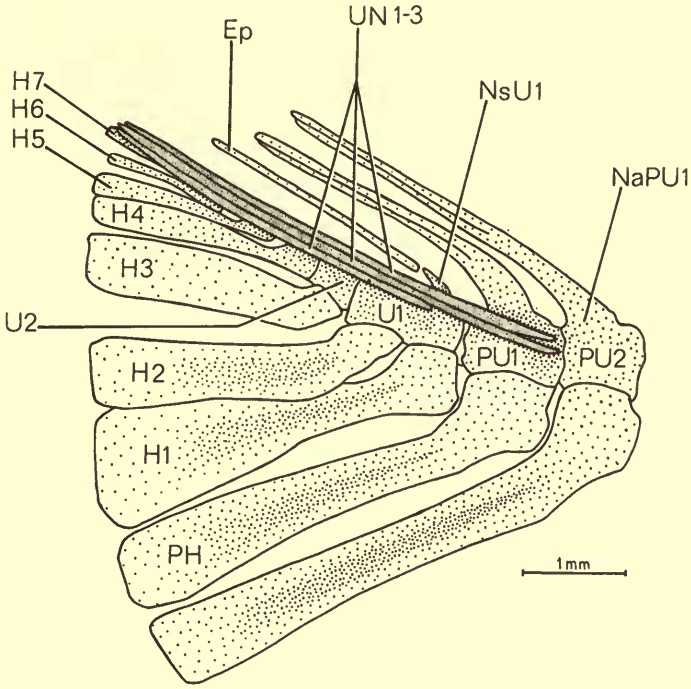

FIG. 9. *Lycoptera middendorffi*. Caudal fin skeleton, drawn from a latex cast of B.M. (N.H.) P16967b. Ep. epural ; H1–7 ; hypurals ; naPUI. neural arch of 2nd preural vertebra ; NsPU1. neural spine of 1st preural vertebra ; NsU1. neural spine of 1st ural vertebra ; PH. parhypural ; PU_1 ; PU_2, 1st and 2nd preural centra. U_1 ; U_2, 1st and 2nd ural centra. UN1–4, uroneurals.

anteriorly. As Saito (*op. cit.*) demonstrated, in a diplospondylous caudal vertebra one hemicentrum of a pair (the anterior) is arch-less, while the other carries a neural and haemal arch and spine. The ural pair each has a neural arch and spine, as well as a hypural (modified haemal arch and spine). This suggests that each " first " ural element is a complete vertebra.

There is no appreciable size difference between individuals with double and single first ural vertebrae. Perhaps, as Patterson (1967) suggested, *Lycoptera* shows individual variability in this character. Gaudant (*op. cit.*) believed that Patterson's observations could be attributed to poor preservation of the material. But I can certainly confirm that this is not so. Indeed, on one slab (P16967a) there are two

specimens, overlapping one another, and both equally well-preserved ; in one fish there is a double " first " ural vertebra, in the other a single centrum.

When the first ural is a single element, only one neural arch and short spine is present, and the same condition is found on those apparently single centra with a clear-cut line of fusion still persisting. Also, when the centrum is a single element, its overall length is somewhat less than the two portions together. These observations seem to indicate that, if fusion is involved in the usual growth process, then there is a certain amount of resorption and remodelling of the bones.

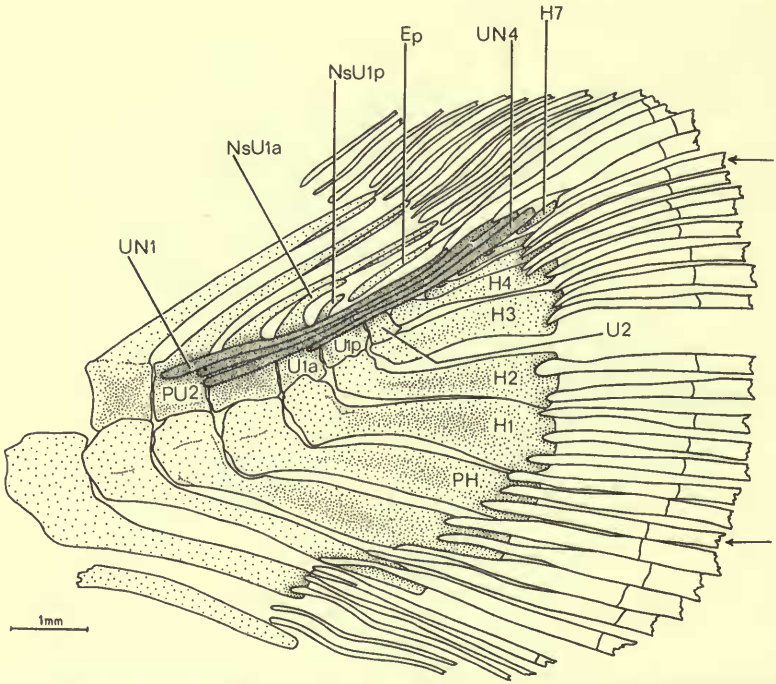

FIG. 10. *Lycoptera middendorffi*. Caudal fin skeleton (from P20930) to show the double " first ural " centrum. The first branched principal caudal ray of each lobe is indicated by an arrow. For abbreviations, see fig. 9 and NsU1a, NsU1p. neural spine on anterior and posterior elements of " first ural " centrum ; U1a and U1p. anterior and posterior components, respectively, of " first ural " centrum.

In all teleosts (as defined by Patterson, 1968) the first ural centrum always carries two hypurals and is therefore to be considered a compound element. The double condition found in certain *Lycoptera middendorffi* individuals would seem to be the retention of a primitive condition, a stage already lost in the other upper Jurassic and lower Cretaceous teleosts (*eg. Leptolepis, Thrissops, Allothrissops*). Other characters of the caudal fin skeleton in *Lycoptera, eg.* perichordally ossified centra, elongate uroneurals extending forward to the preural centra, two hypural support for the lower caudal lobe—preclude arguments that the skeleton is not teleostean.

Returning now to the overall morphology of the caudal skeleton in *Lycoptera*. If

my interpretation of this structure is acceptable, there is a definite resemblance between the caudal skeleton in *Lycoptera* and *Hiodon* ; particularly in three important characters (*cf.* text fig. 8 with figs. 9 and 10).

First, there is agreement in the number of branched principal rays (16) ; other primitive teleosts (including *Leptolepis*) have 17 (*i.e.* 9+8). Sixteen rays are otherwise known from the Hiodontidae and most Mormyridae (see Nelson, 1969 for further discussion ; certain Galaxiidae with 16 rays [see McDowall, 1969] are irrelevant since the caudal skeleton in these fishes eliminates them from consideration as truly primitive teleosts).

Second, there is close similarity in the uroneural arrangement. In *Hiodon* and *Eohiodon* the 3 or 4 long uroneurals are arranged in a single series (that is, there is no upper series of one or more short uroneurals, as is typical for the lower teleosts). Certain other primitive fishes (*eg. Allothrissops, Thrissops,* ichthyodectids) also have only the lower set of uroneurals, but these are far more numerous (up to 7 ; see Patterson, 1967 ; Cavender, 1966b) than in *Hiodon* or *Lycoptera.*

Finally, in both *Lycoptera* and the hiodontids there is only one epural, a most unusual feature in lower teleosts. All other primitive groups (except perhaps the Osteoglossoidei, Notopteridae and Mormyridae, where the epural is probably absent, see discussion in Nelson, 1969) have three epurals (Patterson, 1968).

There is considerable variation is some aspects of the *Hiodon* caudal skeleton, especially in the number and development of neural superstructures associated with the first ural and preural vertebrae. For example, a fully developed spine on the first preural vertebra (present in *Lycoptera*) is not always developed, and the neural spine on the first ural is smaller than in *Lycoptera.* Nevertheless, the overall picture of variation for these characters in *Hiodon* and *Eohiodon* encompasses the condition found in *Lycoptera.* Most specimens of *H. alosoides* and *H. tergisus* have two neural arches on the first ural centrum, a condition reminiscent of that seen in some *Lycoptera,* but probably of no importance other than as a further indication of the compound nature of that vertebra.

Not only in general features, but in at least three critical characters the caudal fin and its supporting skeleton in *Lycoptera* is closer to that of *Hiodon* than to that of any other genus or group of fishes. Resemblances to the *Thrissops*—ichthyodectid caudal skeleton will be discussed elsewhere (but see Patterson, 1968, and Greenwood *et al,* 1966).

Fins and fin girdles. There is not enough information about the pectoral and pelvic girdles in *Lycoptera* for any meaningful comparisons to be made.

The *pectoral fin* of *Hiodon* spp., and *Eohiodon* is more expansive and falcate than that of *Lycoptera,* and has more rays (11–14, and *ca.* 13, *cf.* 9). *Lycoptera* has both the first and last rays enlarged, thickened and unbranched. In *Hiodon* only the first ray is unbranched and noticeably enlarged ; the lowermost ray has, however, a broad, fleshy extension of the membrane along its trailing edge. No details are available for this fin in *Eohiodon.*

Pelvic fin size, shape and area are similar in the three genera ; *Hiodon* species have 7 pelvic rays (the first unbranched), *Eohiodon* about 7 (no other details) and *Lycoptera* spp., 7 to 9.

The *median fins* in *Lycoptera*, *Hiodon* and *Eohiodon* are set well-back on the body ; fin outline is similar in the three genera, although the anal is longer in *Hiodon* (23–32 rays) than in *Lycoptera* (13–20, according to accounts in Yakovlev, 1965). Dorsal fin length is approximately equal (9–12 rays in *Hiodon*, 10–12 in *Lycoptera*). The dorsal fin ray count for *Eohiodon* (12 to 13) lies within the range for *Lycoptera*, as does the count for the anal (15 to 16 rays). In these characters *Eohiodon* shows a somewhat closer resemblance to *Lycoptera* than to *Hiodon*.

Scales. Cockerell (1925) used scale morphology in *Lycoptera* as a basis for defining the family Lycopteridae (as distinct from the Leptolepidae, in which *Lycoptera* had been classified previously). Although the scales of *Lycoptera* are distinctive *vis à vis* those of *Leptolepis*, Cockerell did note their close resemblance to the scales of the European Minnow *Phoxinus phoxinus* (thereby initiating the idea that lycopterids might be cyprinid ancestors).

Lycoptera scales are small, circular or slightly ovoid, with regularly arranged concentric circuli, with radii present basally and apically (the latter less well-defined than the former), and with a distinct, relatively large nucleus.

Hiodon scales are not similar. In outline they are almost thumbnail-shaped, with the anterior margin concave at each corner but convex medially (more so in scales from the flank than the dorsum) and with the laterobasal corners sharply rounded. The circuli are not arranged in circles since they bend to follow the outline of the margin. The nucleus is relatively small. Primary radii are confined to the anterior field, and are more numerous than in *Lycoptera* scales.

Little is known about the scales of *Eohiodon* (see Cavender, 1966a, page 317.)

DISCUSSION

Summary of anatomical features. Many characters shared by *Lycoptera* and *Hiodon* are characteristics of primitive teleosts, and thus are of little value in establishing relationships. Among these are :

1. The arrangement and relationship of bones in the dorsicranium (but see below regarding the temporal fenestra).
2. The pattern of the cephalic lateral line system.
3. Presence of teeth on the parasphenoid and the palatopterygoid arch.
4. Mode of articulation between upper jaw elements.
5. Similarities in the morphology of the vertebrae.

The diplospondylous condition of the centra in (presumably) near adult *Lycoptera* would seem to be more primitive than the monospondyly of *Hiodon*. Nelson (1969) considers the absence of the lower intermuscular bones a specialized feature. Since these bones are not developed in pholidophorids (Lund, 1966), nor in primitive teleosts like the leptolepids and ichthyodectids (including *Thrissops* and *Allothrissops*), I cannot agree with Nelson's conclusion.

Certain characters are less readily classified as primitive or derived. Among these perhaps should be included the infraorbital bones. Nelson (1969) suggests that the six infraorbitals in the Osteoglossomorpha (including *Hiodon*) probably represent a specialized condition *Lycoptera* seems to have the primitive number of seven (see page 270) but the elongate and slender lachrymal (1st infraorbital) is not typically

that of the more primitive teleosts, and closely resembles the lachrymal of *Hiodon*. In these other fishes the lachrymal is stouter and deeper than in *Lycoptera* (see for example the figures of *Leptolepis* and *Thrissops* in Patterson [1967], and those of *Elops* and *Albula* in Nelson [1969, text fig. 7]). The infraorbitals of *Lycoptera* could well provide the basic type from which the *Hiodon* pattern evolved by the fusion of bones 3 and 4 (see Nelson, *op. cit.*) and the posterior extension of the 5th bone. The specialized condition of the *Lycoptera* antorbital is discussed above. The absence of a supraorbital bone in both *Hiodon* and *Lycoptera* is an unusual and probably a phyletically significant feature.

The reduced number of branchiostegal rays (*ca.* 8–10) in *Lycoptera* is certainly an advanced character. That this number is identical with the number occurring in *Hiodon*, and that both genera have the ceratohyal and branchiostegal rays of a similar shape, can I think be taken as evidence indicating relationship. A review of branchiostegal and ceratohyal shape in lower teleosts (including fossil taxa where this bone is preserved) brings to light no other species with branchiostegals and ceratohyal as similar to those of *Lycoptera* (personal observations, and McAllister, 1968). *Hiodon* has two hypophyals on each side (a primitive feature) but *Lycoptera* has only one (see page 272).

There is a marked similarity in the shape of the parasphenoid of *Lycoptera* and *Hiodon*, particularly with respect to the steep angle made between the orbital and occipital limbs of the bone. Such a sharply angled skull-floor is probably unique among primitive teleosts. The presence of a basipterygoid process on the parasphenoid of *Lycoptera* is, of course, a primitive feature lost in *Hiodon*.

Parapophyses fused with the vertebral centra is a specialized characteristic. In *Hiodon* the pleural ribs articulate with the centrum or with the parapophysis base where it is fused with the centrum. *Lycoptera*, although having fused parapophyses, retains the more primitive condition of ribs articulating with the tips of the parapophyses. It is noteworthy that in both *Hiodon* and *Lycoptera* the vertebral organization in general is primitive, yet the parapophyses are firmly fused with the centrum.

If my identification of the large otolith in *Lycoptera* as a lapillus is correct (see page 269), then there is a remarkable degree of similarity between the two genera in a most unusual specialization. Little is known about this otolith in lower teleosts, but no living elopomorph, osteoglossomorph or primitive euteleostean has a lapillus as like that of *Lycoptera* as is the lapillus of *Hiodon*.

There remain two characters, the caudal fin skeleton and the lateral temporal fenestra. These I consider to have great import in establishing a phyletic relationship between the lycopterids and hiodontids.

Although primitive characters persist in the caudal skeleton of *Hiodon* and *Eohiodon* (as for example a separate second ural centrum and seven hypurals) there are two other features which can only be considered derived ones. These are the single epural, and a reduction in the number of principal branched caudal rays to sixteen. In the primitive caudal fin there are three (rarely two) epurals, and seventeen branched rays (for further discussion see Greenwood and Patterson [1967], and Nelson [1969]). Another unusual feature, but one shared with some Mesozoic Ichthyo-

dectidae (Patterson, 1968), is the arrangement of the uroneurals into a single series of elongate elements (see page 277).

In combination, the single uroneural series, the single epural, and the sixteen caudal rays of *Lycoptera* are otherwise found only in *Hiodon* and *Eohiodon*.

Likewise, a temporal fenestra bordered by the parietal, pterotic and epiotic is found only in *Lycoptera* and *Hiodon* (the condition in *Eohiodon* is unknown).

TAXONOMIC CONSIDERATIONS. On the basis of their shared specialized characters, I would conclude that the Lycopteridae are more closely related to the Hiodontidae than to any other group of teleosts. Several primitive features, lost in the Hiodontidae, are present in the Lycopteridae, which should therefore, be considered the plesiomorph sister group of the Hiodontidae.

In turn, the lycopterids and hiodontids together constitute a plesiomorph sister group to the more specialized Notopteridae. These relationships are perhaps best expressed by uniting the Hiodontidae and Lycopteridae in one superfamily (Hiodontoidea ; new taxon), and by creating another superfamily (Notopteroidea) for the Notopteridae. Both superfamilies can be included within the suborder Notopteroidei (order Osteoglossiformes) of Greenwood *et al*, 1966.

These conclusions are at variance with the opinions expressed by previous students of the Lycopteridae. Of these workers, five suggested (with varying degrees of confidence) relationship with the Cyprinidae (Cockerell [1925] ; Gregory [1933] ; Saito [1936] ; Takai [1944] ; Liu *et al* [1963]), three favoured affinity with the basal Clupeiformes *sensu* Berg (1940) (Berg [1948] ; Lehman [1966], Gaudant [1968]) and one, Yakovlev (1965), with the Osteoglossidae.

Evidence for relationship between the Lycopteridae and the Cyprinidae stems chiefly from similarity in scale morphology (Cockerell *op. cit.*) and from Reis' (1910) identification of the largest otolith as an asteriscus, thus implying a cyprinoid type of inner ear. However, no other anatomical or gross morphological features can be adduced to support this postulated relationship, and doubt can be thrown on the otolith evidence (see above, page 267). In all features generally thought to be important indicators of phyletic relationship (especially the caudal fin skeleton) the cyprinids and lycopterids are very distinct, and the same may be said for the other ostariophysan families (see Rosen and Greenwood, 1970).

A relationship between the Lycopteridae and certain basal teleosts (*i.e.*, the more primitive members of Berg's [1940] order Clupeiformes, such as the elopoids and leptolepoids) seems, at first sight, to be more reasonable. But again, apart from similarities in basic, primitive features the lycopterids differ in many important ways (caudal skeleton, number of branchiostegals, morphology and relative size of the otoliths, presence of a temporal fenestra, etc.) To classify the lycopterids with Berg's Clupeiformes would seem totally to disregard their phyletic affinities.

Yakovlev's (*op. cit.*) suggested relationship of *Lycoptera* with the osteoglossid *Arapaima* is of particular interest. However, the shared characters which Yakovlev lists are not critical ones ; most are primitive features found in all basal teleosts (a medioparietal skull, basipterygoid process on the parasphenoid, teeth on parasphenoid and basihyal plate). Of the others, I would doubt whether the nasals are contiguous in *Lycoptera* (see page 261), and a large opercular process occurs in other

and unrelated lineages (see page 272). That *Lycoptera* is a member of the Osteoglossomorpha seems certain, but the nature of its caudal skeleton militates against its inclusion in the Osteoglossoidei (Greenwood, 1967 ; Nelson, 1969).

ZOOGEOGRAPHICAL IMPLICATIONS. Nelson (1969) has discussed at length evidence relating to the phyletic and geographical history of the Osteoglossomorpha. Important lacunae in this evidence concern the primary area of distribution, and the interrelationships, of the Hiodontidae. The lycopterid—hiodontid relationship proposed above does little to fill this gap except to strengthen the hypothesis that the hiodontid lineage was probably of north-eastern Asiatic origin. The problem of hiodontid–notopterid interrelations, and other aspects of osteoglossomorph geography will be reviewed in a forthcoming paper.

Weiler (in Martin and Weiler, 1954, 1957 and 1965) has referred a number of different otoliths, from the Mesozoic of Germany, to the suborder Lycopteroidei (*sensu* Berg, 1940). Like other authors, Weiler based his comparisons on Reis' (1910) figures. Even allowing for the difficulties inherent in this procedure, I cannot see a close resemblance between the German and Siberian otoliths ; none of the specimens figured by Weiler shows the characteristic outline and sculpturing of the larger otolith in *Lycoptera*. Thus, on the evidence of otoliths alone, it would by unwise to assume that lycopterid fishes occurred in Europe during the Mesozoic.

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SUMMARY

A comparative osteological study of the Mesozoic genus *Lycoptera* and members of the family Hiodontidae, indicates a close relationship between the two taxa. Of particular importance in this regard are the nature of the caudal fin skeleton, the number of caudal fin rays, the presence of a temporal fenestra, and details of the hyoid arch skeleton.

The peculiar otoliths of *Lycoptera* seem to resemble those of *Hiodon* and it is suggested that, contrary to earlier opinions, the inner ear of *Lycoptera* was probably of the *Hiodon*-type and not the cyprinid type.

Previous views on the relationships of the Lycopteridae are reviewed. No evidence can be found to support the idea that the Lycopteridae are ancestral cyprinids or that there is any relationship between the elopoid lineages and the Lycopteridae.

It is suggested that the Lycopteridae and Hiodontidae be placed in one superfamily, the Hiodontoidea, and that the apomorph sister group of this taxon is the superfamily Notopteroidea (containing only the Notopteridae).

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